

REVISION OF THE RHAMNUS SERRATA COMPLEX

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While I was working on a revision of *Rhamnus* as found in Mexico and southward, my interest was captured by a small group of closely-related species that have narrowish shiny leaves, bud scales, four-merous flowers that are solitary or in axillary clusters of two or three (rarely four) and that tend to be unisexual, and glabrous two-seeded fruits. I call this group informally the *Rhamnus serrata* complex, and I find it especially interesting and exasperating because of the puzzling populations in northern Mexico and western Texas. These are ambiguous, suggesting relationships, on the one hand, to the Coloradan and New Mexican plants called *R. smithii* Greene and, on the other, to *R. serrata* Schult. of the central Mexican highlands. The latest monographer of the group, C. B. Wolf (The North American Species of *Rhamnus*, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 1-136. 1938) called the plants of Colorado and northern New Mexico *R. smithii* ssp. *typica* and those of southern New Mexico and western Texas *R. smithii* ssp. *fasciculata* (Greene) Wolf. That he did not consider the latter taxon more nearly related to *R. serrata* is apparently a function of the real or fancied geographic proximity of the populations of southern New Mexico to those of northern New Mexico and the fact that *R. serrata* had at that time not been found north of San Luis Potosí. The few poor collections available to Wolf did not reveal a taxonomic problem to him. In the years after Wolf's monographic work, botanical exploration began to show the occurrence of plants of this affinity in several areas of northern Mexico. Collections have been made from a number of mountain masses that, though still leaving some small gaps, very nearly "connect" the central Mexican area with the Rocky Mountain area and reveal the ambiguous taxonomic position of the plants between them (Fig. 1). Examination of about five times as many collections of this complex as were studied by Wolf now suggests that the Mexican *R. serrata* extends in some of its numerous local forms to southern New Mexico and to two localities in Arizona (thus embracing the *R. fasciculata* Greene), but that the northern New Mexican and Coloradan plants are still best treated as a distinct species, *R. smithii*. The latter, in fact, on the basis of length of leaves and petioles, color of leaves beneath, characteristics of the leaf margin, and time of anthesis, seems more closely related to *R. lanceolata* Pursh, a species of lowland forests of eastern United States (Fig. 1).

As will be evident from the following key, and from Wolf's key, the distinctions are tenuous and difficult to put down on paper. One valid alter-

native to my recognition of several species is to submerge all the members of this complex as varieties of *R. lanceolata*. This would create a wide-ranging and somewhat diverse species such as has been done for the *Prunus serotina* complex (R. McVaugh, *Brittonia* 7: 279-315. 1951), for the *Ptelea trifoliata* complex (V. L. Bailey, *Brittonia* 14: 1-45. 1962), and for the *Cercis canadensis* complex (M. Hopkins, *Rhodora* 44: 193-211. 1942). But on the other hand the species that I recognize here are as well marked as those in other sections of *Rhamnus*, and there appears to be little to gain from the more inclusive approach.

An ancillary problem is presented by *R. standleyana*, based by Wolf on a single collection (*Purpus* 4968) from a seldom-visited mountain range in Coahuila. The general habit of growth and the very small leaves, sometimes fascicled, suggest that this is indeed a distinct taxon. Lending support to this thesis is another specimen from another range in Coahuila (*Johnston* 9031), which seems to me to belong to this category. In other characters (e.g., moderate number of very short almost invisible hairs on both leaf surfaces, yellowish color of undersurface of leaf, and prominent sharp-pointed marginal serrations) these plants appear to be so similar to other members of *R. serrata* that they could be considered a variety thereof. However, until field study and other techniques can be used to clarify the relationships, I do not feel justified in making a new combination for these two specimens and will follow Wolf's nomenclature, as in the following key.

- 1a. Shrub usually more than 1 m high, the branchlets averaging longer than 1.5 cm and leaves averaging longer than 1.2 cm and not fascicled 2
- 1b. Small shrubs with branchlets averaging about 1.5 cm long and leaves all under 1.2 cm long, fascicled or tending toward fasciculate. 4. *R. standleyana*
- 2a. Stipules quickly deciduous or somewhat persistent but only rarely at leafless nodes, averaging more than 3 mm long; below 3000 m. . . . 3
- 2b. Stipules abundant, persistent even at leafless nodes, averaging less than 3 mm long; Guatemala above 3000 m. 3b. *R. serrata* var. *guatemalensis*
- 3a. Branchlets often long, averaging 5 cm or more in length; eastern United States below 1000 m. 1. *R. lanceolata*
- 3b. Branchlets shorter; at higher elevations, not in eastern United States 4
- 4a. Upper surface of leaf gray or olive-green, lower surface paler, rarely yellowish; bud-scales thin, pale; southern Colorado and northern New Mexico 2. *R. smithii*
- 4b. Upper surface of leaf green, lower surface yellowish to brownish, rarely paler green; bud-scales coriaceous, dark reddish; Chiapas northward through western Texas, southern New Mexico, and Arizona. 3a. *R. serrata* var. *serrata*

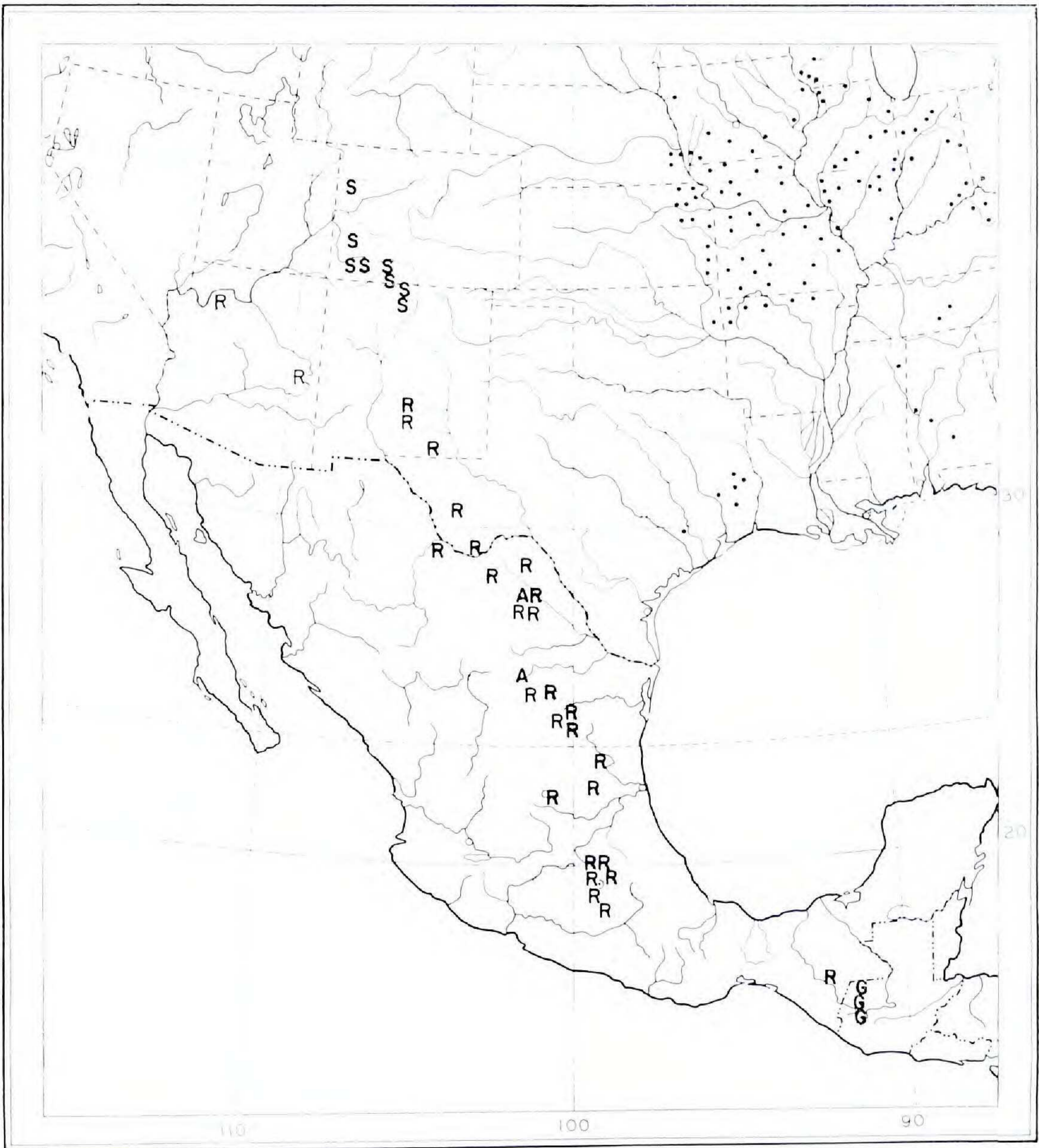


Fig. 1. Documented distribution of members of the *Rhamnus serrata* complex. A, *R. standleyana*; G, *R. serrata* var. *guatemalensis*; R, *R. serrata* var. *serrata*; small dots, *R. lanceolata*, incomplete distribution, the species occurring as far east as Pennsylvania, Maryland, and Virginia.

1. RHAMNUS LANCEOLATA Pursh, Fl. Amer. Sept. 1: 166. 1814.

Sageretia lanceolata (Pursh) G. Don, Gen. Syst. 2: 29. 1832.

Rhamnus shortii Nuttall, J. Acad. Nat. Sci. Philadelphia 7: 91. 1834.

Rhamnus parvifolius Torrey & Gray, Fl. North Amer. 1: 262. 1838.

Cardiolepis nigra Raf., First Cat. Bot. Gard. Transylv. Univ. 18. 1824, nom.; Neogen. 1. 1825; Sylv. Tellur. 28. 1838.

Cardiolepis rubra Raf., Neogen. 1. 1825; Sylv. Tellur. 28. 1838.

Sarcomphalus shortianus Raf., Sylv. Tellur. 29. 1838.

Shrub usually about 2 m high but at times larger, deciduous; bark greenish and sparsely to moderately beset with short hairs when young, reddish and glabrous when older with a thin broken or peeling light-colored outer layer; branchlets frequently long and whip-like with distal leaves larger than proximal and not crowded; bud-scales 1–1.75 mm long and 1–2 mm broad, deltoid, dark reddish, tough and brittle when dried, apically acute or obtuse, with marginal hairs at apex only. Leaves mostly more than 3 cm long when mature, 2–3.5 times as long as broad, at apex acuminate on the large distal leaves through acute on medium-sized leaves to obtuse on small proximal leaves of a branchlet, beneath somewhat paler green than or occasionally the same as above, above and beneath glabrous or with a few hairs which are sometimes visible only when the leaf is at an angle and either short on both surfaces or longer beneath than above; nerves usually glabrous above and with some hairs beneath, and beneath either dark- or light-colored and conspicuous or not; marginally plane (rarely revolute), crenate or occasionally serrate, the teeth (6–)8–18 per cm and with or without dark-colored apexes; leaves thin and easily flexible; petioles (2–)3–6(–8) mm long (longer on type specimen) and usually with hairs only on the margin of an anterior furrow; stipules lorate, 3–5(–6.5) mm long, 0.5 mm broad, pale yellowish, thin and flexible and quickly deciduous. Flowers unisexual, associated with immature leaves, in clusters of 1–3 in the axils mainly of small proximal leaves; pedicels (1–)2–3 mm long, glabrous; floral cup (1–)1.5–2.5 mm deep, 1–1.5 (–2) mm broad, deeper than broad, campanulate or funnelform (rarely hemispheric); sepals 4, ca. (1.25–)1.5–2 mm long, 1–1.25 mm broad, longer than broad; petals 4, ca. 1 mm long and broad (smaller in pistillate flowers), the broad portion gradually narrowing to form a claw in staminate flowers, broadly notched, uniformly colored; style of pistillate flowers ca. 2 mm long, exerted, bifurcate a fourth its length; filament of staminate flowers ca. 1 mm long, broadly based, the anther small and entirely enclosed by petal in pistillate flowers and partially exposed in staminate ones. Fruit 1–2 usually in axils of small proximal leaves of a branchlet, glabrous, 2-seeded (a few with 3 carpels at an early stage but one aborting), 4–5 mm in diameter (to 7 mm *vide* Wolf), either globose or somewhat prolate, black; pedicels up to 4 mm long, about 1 mm longer than at anthesis; floral cup glabrous and with margin entire or with 2 notches.

In moist wooded areas at less than 1000 m. The map (Fig. 1) shows a rather continuous distribution in the midwestern states but rather large disjunctions in the South. The most striking hiatus, apparently real and not simply the result of inadequate collecting, is from eastern Texas to Alabama and northeastern Oklahoma or northwestern Arkansas, a gap of well over 500 km. The species is unknown in Louisiana and in the southern four-fifths of Arkansas.

Rhamnus lanceolata var. *glabrata* Gleason (Phytologia 2: 288. 1947) seems to be no more than a trivial pubescence form.

TYPE: United States: Tennessee: *Lyon s.n.* (PH!).

REPRESENTATIVE SPECIMENS: United States: Arkansas: *Moore s.n.* (TEX, WIS). Illinois: *Umbach 8349* (TEX, WIS). Indiana: *Friesner 18795* (TEX). Iowa: *Davidson 546* (TEX). Kansas: *McGregor E375* (TEX, WIS). Kentucky: *Short s.n.* (WIS); *Wharton 10844* (NA). Maryland: *Lyon s.n.* (PH). Mississippi: *Ray 8226* (WIS). Missouri: *Hardin 666* (TEX). Nebraska: *Osborn 772R* (MO). Pennsylvania: *Davis 7061* (MO). Tennessee: *Quarterman 4010* (NA). Texas: *Palmer 5180* (US); *Lindheimer 161 = exs. II 228* (MO). Virginia: *Lyon s.n.* (PH).

2. RHAMNUS SMITHII Greene, Pittonia 3: 17. 1896.

Rhamnus smithii subsp. *typica* C. B. Wolf, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 56. 1938.

Shrub 1–2 m tall, deciduous; branchlets (1.5–)2–4(–6) cm long with 6–8(–11) leaves and internodes averaging about 3 mm in length with moderate numbers of short hairs; bark greenish, smooth, with moderate numbers of short hairs when young to grayish and rough and glabrous or sparsely hairy when older and often with a thin, white exterior layer; bud-scales 2.5–6 mm long, pale, flexible, with fimbriate margin and acute or obtuse or notched apex. Leaves 1–1.5 cm long, 0.5–0.6 cm broad on flowering specimens (immature), 4–7.5(–8) cm long, 1.3–2.7(–3.3) cm broad when mature, (2.2–)2.4–2.7(–3.5) times longer than broad, at apex obtuse (usually on smaller leaves) or acute (usually on larger leaves), above gray- or olive-green, beneath paler than or occasionally the same as above or rarely yellowish or yellowish brown on older leaves, on both surfaces glabrous or apparently glabrous with scattered short erect hairs that are invisible when leaf surface is viewed at right angles; nervature above and beneath glabrous or with a few short hairs, beneath dark colored with rare exceptions and conspicuous; margins plane or occasionally slightly revolute, crenate or crenulate with (7–)9–15(–17) usually remote teeth that are apically amber colored to colorless; texture thick or semi-thick and barely flexible; petioles (2–)3–6(–8) mm long with short to medium-length erect hairs usually more heavily concentrated along a ventral furrow; stipules (2.5–)3–4(–5.5) mm long, 0.5 mm broad, pale brownish, membranous, with scattered marginal hairs, quickly deciduous. Flowers associated with immature leaves, 1–3(–4) per axil, either unisexual or protandrous (only appar-

ently staminate flowers seen), pedicels 1.5–2.5 mm long, with sparse to moderate amounts of short, erect hairs; floral cup (1–)1.5–2 mm long, (0.75–)1–1.75 mm broad, longer than broad, campanulate to funnelform, glabrous, dark-colored; sepals 4, 1.25–1.5(–2) mm long, ca. 1 mm broad, longer than broad, glabrous, pale colored; petals 4, ca. 1 mm long, 0.75 mm broad, the broad part gradually narrowing to form a claw, narrowly and acutely notched, mostly uniformly colored or a few with darker-colored upper portion; style bifurcate about half its length; stamens 4, the filaments broad based, each enclosed by a petal, the anthers ca. 0.5 mm long, from half to completely exposed above petal, uniformly yellow; ovary glabrous. Fruit 1–2 per axil of small proximal leaves usually, glabrous, 2-seeded, (3–)4–6(–8) mm long and either globose or somewhat longer than broad, appearing mostly dark brown when dry, the floral parts either absent or a very short portion of the style retained, the floral cup shallow with two notches or less frequently entire and sparsely to moderately beset with short, erect hairs, and pedicels ca. 1 mm longer than at anthesis.

On dry hillsides or along streams usually between 2000 and 2500 m but rarely up to 3000 m. It is known in Colorado and New Mexico (Fig. 1). The report of its occurrence in Arizona (T. H. Kearney and R. H. Peebles, *Arizona Flora*, p. 532, 1951) is based on a specimen now referred to *R. serrata*.

TYPE: United States: Colorado: Pagosa Springs, *Smith s.n.* (PH!)

REPRESENTATIVE SPECIMENS: United States, Colorado: *Andrews s.n.* (PH, US); *Baker 458* (POM, US); *Bethel, Willey, & Clokey 4197* (PH, POM, US); *Brandegge s.n.* (PH); *Cary 172* (US); *Eastwood 17* (POM, US); *Eggleston 14182* (US); *Graham 9709* (US); *Payson 113-7* (TEX); *Tucker 3226* (UCLA); *Vasey s.n.* (US); *Waterfall 15146 & 11710* (RSA); *Weber & Livingston 6333* (RSA, TEX); *Wolf 3082* (RSA, UCLA, US); *Wooton 2899* (US). New Mexico: *Eggleston 6483 & 6566* (US); *Standley 6835* (US).

3. RHAMNUS SERRATA Humb. & Bonpl. ex Schult. in R. & S., Syst. 5: 295. 1819.

Two varieties can be discerned, distinguished by those characters noted in the key; each of the varieties is described and treated below.

3a. RHAMNUS SERRATA Schult. var. SERRATA

Rhamnus serrulata H.B.K., Nov. Gen. et Sp. 7: 51. t. 617. 1825.

Rhamnus fasciculata Greene, Leaflet Bot. Observ. Crit. 1: 63. 1904.

Rhamnus smithii subsp. *fasciculata* (Greene) C. B. Wolf, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 58. 1938.

Rhamnus smithii subsp. *fasciculata* var. *mulleri* Fosberg, Lloydia 4: 286. 1941.

Shrub from 1–3(–5) m tall, deciduous or evergreen; bark greenish or when young reddish, grayish or brownish when older with hairs short to long (long only in Texas and most Coahuila collections), mostly erect and straight, of usually moderate amount sometimes glabrate with age (bark

observed to be rough and scaly on a collection from western Texas and several from Coahuila and some from Nuevo León); branchlets (0.6–)0.9–9.5(–12) cm long (the average being about 1–2.5 cm), (4–)6–8(–14) leaves per branchlet; bud-scales 1–2 mm long, coriaceous, dark reddish, with apex broadly obtuse and with hairs dorsally (collections from New Mexico, Texas, and Coahuila) or marginally only (from farther south). Leaves (0.3–)0.5–4(–8.4) cm long with the shorter leaves usually proximal on the longer branchlets or throughout the shorter ones, (0.1–)0.4–1.5(–2) cm broad, from broadly elliptic and ovate (the small leaves, usually) to oblong and lanceolate, at base cuneate to rounded, at apex mostly acute or obtuse (some apices acuminate in the Chiapas collection; some retuse in a few collections from farther north), above green and in most cases either actually or apparently glabrous (hairs, when present, usually visible only if leaf surface is at an angle to the lens, short and mostly erect), beneath yellowish to brownish (a few New Mexico collections show simply paler green undersurfaces) and either actually or apparently glabrous or with moderate numbers of usually short, erect hairs; nervature above inconspicuous or conspicuously pallid and either glabrous or with variable numbers of mostly short, erect hairs and with midvein hairy and secondary nerves with the same amount of hair or less (rarely glabrous), the hairs erect and of variable lengths; margins revolute or plane (revolute more commonly to the South and plane more commonly to the North), usually serrate but sometimes crenate with (6–)10–15(–17) teeth per cm having apices all colorless or amber colored or dark and sometimes prominently large; texture from thin and flexible to firm and moderately thick; petioles 1–4(–5) mm long with moderate numbers of short to moderately long erect hairs which may be confined to or concentrated on the margin of a ventral furrow; stipules 2–5(–6) mm long and about 0.5 mm broad, pale-colored (usually reddish) and either thin or moderately thick with sparse to moderate numbers of hairs which may be exclusively on the margin or midvein and either quickly deciduous or somewhat persistent (rarely at leafless nodes). Flowers associated with mature leaves, monoecious or polygamodioecious or protandrous, 1–3 (rarely 4 or 5) per axil; peduncles absent; pedicels usually 3 mm long or shorter (rarely up to 6 mm); floral cups varying in shape from funnelform through urceolate and campanulate to hemispheric (the latter uncommon), (0.6–)1–1.5(–2) mm deep (usually shallower in pistillate than in staminate flowers), 1–2 mm broad, usually broader than deep, glabrous or with sparse to moderate numbers of short, erect hairs; sepals 4, ca. 1–2 mm long, 0.6–1.5 mm broad (usually smaller in pistillate than in staminate flowers), glabrous or with sparse to moderate pubescence; petals 4, ca. 0.5–1.1 mm long, 0.5–1 mm broad at widest part (smaller in pistillate than in staminate flowers), claw apparently more distinct in pistillate flowers, with a notch a fourth to a third the length of the petal, uniformly colored or with the distal portion darker; anther 0.5–0.75 mm long (shorter in pistillate flowers), enclosed by petal partially in staminate flowers and com-

pletely in pistillate flowers. Fruit 1–2 per axil, glabrous, 2-seeded, (3–)4–6(–8) mm broad, either globose or somewhat prolate, pedicels (1.5–)2–4(–6) mm long and with usually moderate pubescence; floral cup with margin circular or split into two parts and glabrous or with short hairs; style sometimes retained.

Found from 1200 to 3000 m.

TYPE: Mexico: *Humboldt & Bonpland s.n.* (B-WILLD No. 4637!)

REPRESENTATIVE SPECIMENS: United States: Arizona: *Hevly s.n.* (ARIZ); *Schroeder s.n.* (ARIZ). New Mexico: *Bailey 454* (US); *Barlow s.n.* (UCLA); *Goodding 6574* (ARIZ); *Eggleston 14361 & 14366* (US); *Hinckley 6567* (ARIZ); *Rehder 427 & 431* (US); *Standley 40687* (US); *Vaughan 1798 & 1799* (ARIZ); *Wolf 2784* (RSA, UCLA); *Wolf 2824* (POM, UCLA, US); *Wooton s.n.* (ARIZ, POM, US); *Wooton 203* (POM, US). Texas, *Correll 29751* (TEX); *Correll & Hanson 29821* (TEX); *Ferris & Duncan 2528* (CA, DS); *Havard 129* (US); *Hinckley s.n. & 985a* (TEX); *Marsh s.n. & 354* (TEX); *McVaugh 7445* (TEX); *Moore & Steyermark 3161* (CA, UC, US); *Palmer 30919 & 31992 & 34337* (US); *Tharp, Warnock, & Hinckley s.n.* (TEX); *Warnock 1023 & 6843 & 12713* (TEX); *Warnock & Tharp 5100 & 6843* (TEX).

Mexico: Coahuila: *Graber 135* (TEX); *Johnston, Chiang, Wendt, & Riskind 11859* (TEX); *Johnston et al. 9393 & 11240 & 11886 & 11924* (TEX); *Marsh 1938* (F, TEX); *Marsh 1389* (F, GH, TEX); *Johnston & Muller 597* (MICH, MEXU, TEX); *Muller 3188* (GH, NA); *Pringle 2810* (GH); *Warnock 11604* (TEX). Chihuahua: *Johnston et al. 10754* (TEX). Tamaulipas: *Sullivan 590* (ENCB, TEX); *Webster 134 & 146* (TEX). Nuevo León: *Johnston et al. 11051* (TEX); *Muller 399 & 455 & 846* (A, F, MICH, TEX); *Muller 1034* (A, TEX); *Muller 2872* (GH, NA); *Taylor 98* (ARIZ, F, TEX); *White 1485* (ARIZ, GH, MICH, US). San Luis Potosí: *McVaugh 10454 & 22161* (MICH); *Palmer 57 & 214* (F, GH, US); *Parry & Palmer 116* (GH, NA, US); *Pennell 17810* (US); *Purpus 5330* (F, GH, MEXU, US); *Rzedowski 4504 & 8050* (ENCB); *Rzedowski 6818* (ENCB, TEX); *Rzedowski 7741* (ENCB, MICH, TEX). Hidalgo: *Chiang et al. 8128* (TEX); *Rzedowski 22190 & 22937* (ENCB, MICH). State of Mexico: *Ehrenberg 979.6* (US); *Paray 361* (ENCB); *Rzedowski 22021* (ENCB, F, MICH, TEX); *Rzedowski 24180 & 28525* (ENCB); *Rzedowski 28825* (ENCB, MICH); *Uhde 1163 & 1169* (US). Distrito Federal: *Bourgeau 698* (US); *Espinosa 710* (ENCB, TEX); *Pringle 8055* (A, F, MEXU, MICH, POM, US); *Pringle 11947* (F, GH, mixed with *Rhamnus mucronata* Schlecht.); *Paray 1907* (ENCB); *Reiche s.n.* (MEXU, US); *Rose & Hough 4233* (US); *Rzedowski 981 & 2266* (ENCB); *Rzedowski 27245* (ENCB, MICH, TEX). Morelos: *Lyonnet 745*. Chiapas: *Laughlin 1784* (TEX).

3b. RHAMNUS SERRATA Schult. var. *guatemalensis* L. A. Johnst., var. nov.

Frutex 0.3–3 m altus sempervirens cortice modice pubescenti pilis brevibus; ramuli (1.5–)3–9(–16) saepissime ca. 4.7 cm longi arcuati saepe

modice laxi; internodia (0.1–)0.2–1(–1.5) saepissime 0.2–0.3 cm longa; squamae gemmae 1–2 mm longae ferruginosae coriaceae apice late obtusae nonnunquamque incisuratae marginae pubescentes. Folia (0.6–)1–4.2 cm longa (0.3–)0.4–1.2(–1.7) cm lata longissima saepissime 3.07 cm longa 1.32 cm lata parvissima saepissime 1.33 cm longa 0.51 cm lata saepe duplo nonnunquam 3.3-plo raro 3.7-plo longiora quam lata crassiuscula supra nitida pilis modice abundis brevissimis fere invisibilibus raro absentibus subtus fere concoloria glabra vel rarissime pilis brevissimis margine revoluta obtuse serrata crenatave dentibus saepissime introrsis mucronibus praesentibus vel nullis; nervi supra glabri subtus glabri vel pubescentes; costa subtus flavescens; petioli 1–2.5(–3.5) mm longi; stipulae tenues pallidae 2–3.5 mm longae 0.5 mm latae pilis sparsis multis persistentibus. Flores axillares; petalae omnes unicolores. Fructi glabri 2-spermi, pedicelli 2.5–4 mm longi pilis modice abundis brevissimis erecti.

Shrubs 0.3–3 m tall, evergreen (leaves present in December and January collections), bark with moderate amount of short pubescence; branchlets (1.5–)3–9(–16) cm long (averaging about 4.7 cm), with curving habit, generally not very crowded (exception: *Molina 21222*); internodes (0.1–)0.2–1(–1.5) cm long, most frequently ca. 0.2–0.3 cm long; bud-scales 1–2 mm long, at apex broadly obtuse and occasionally notched, dark rust-red, coriaceous, with marginal hairs. Leaves (0.6–)1–4.2 cm long, (0.3–)0.4–1.2(–1.7) cm broad, the largest averaging 3.07 cm long, 1.32 cm broad, the smallest averaging 1.33 cm long, 0.51 cm broad, mostly twice as long as broad, at times to 3.3 times and rarely 3.7 times as long as broad, thickish, at apex acute, above lustrous with a moderate amount of very short almost invisible pubescence or rarely glabrous, beneath about the same color as above and glabrous or very rarely with short hairs, at margin revolute, bluntly serrate (the teeth introrse, with rare exceptions) or crenate and with mucros present or absent; petioles 1–2.5(–3.5) mm long, with dense pubescence along the ventral suture, sparser pubescence elsewhere with short hairs; stipules thin, pallid, 2–3.5 mm long, 0.5 mm broad, persistent, with scattered hairs. Flowers (only one seen) axillary; petals uniformly colored. Fruits glabrous, 2-seeded (rarely 3-seeded on an otherwise 2-seeded specimen); stigma retained, bifurcate or trifurcate; floral cup retained either circular marginally or notched on two sides; pedicels 2.5–4 mm long with moderate amount of very short, erect pubescence.

In *Juniperus* woods, on rocky slopes and limestone bluffs at 3300 m most frequently but up to 3900 m at times.

TYPE: Guatemala: Huehuetenango: Sierra de los Cuchumatanes, vicinity of Tunima, *Steyermark 48377* (holotype, A!, isotype, F!).

OTHER SPECIMENS SEEN: Guatemala: Huehuetenango: *Johnston 1778* (F); *Molina 21222* (F); *Molina, Burger &, Wallenta 16477* (F); *Standley 81741 & 81769* (F).

4. RHAMNUS STANDLEYANA C. B. Wolf, Rancho Santa Ana Bot. Gard. Monogr., Bot. Ser. 1: 51. 1938.

Small shrub (probably less than 1 m high); bark reddish and fairly smooth, with short hairs; primary branches long; secondary branchlets short, 0.3–0.4 cm long, averaging about 0.6 cm, with (3–)4–12 leaves per branchlet; internodes 0.1–0.6 mm long or leaves tending to be fascicled; bud-scales minute and brown. Leaves 0.3–1.2 cm long, 0.2–0.5(–0.7) cm broad, about 1.5 to 2.5 times as long as broad, thickish, at apex obtuse or tending to be obtuse, above green, beneath yellowish, above and beneath with moderate amounts of very short pubescence that is almost invisible when leaf is flat, at margin plane and serrate with teeth that are antrorse and slender and apically sharp-pointed and colorless; nervature with short hairs; petioles 1–2 mm long with moderate amount of short pubescence; stipules quickly deciduous. Flowers unknown. Fruit solitary in the leaf axils, glabrous, 2-seeded, ca. 6 mm in diameter, the retained portion of the floral cup with scattered short hairs and entire margin; pedicels 2–4 mm long with scattered short hairs.

Found from about 2500 to 3000 m in limestone sierras.

TYPE: Mexico: Coahuila: Sierra de la Paila, *Purpus* 4968 (F, GH, US)

OTHER SPECIMEN SEEN: Mexico: Coahuila: *Johnston* 9031 (GH).

DISCUSSION

In a species with as large a range as *R. serrata*, morphological and other diversity can be expected. I have delimited only two varieties, but I shall discuss certain geographic patterns and show affinities with the other species treated in this paper.

In the first place *R. smithii* and both varieties of *R. serrata* comprise shrubs usually 1–3 m tall, but shrubs up to 4–5 m have been recorded by collectors in San Luis Potosí and Hidalgo, although this great stature does not seem to correlate with any other distinctive features. *Rhamnus standleyana* is evidently shorter than 1 m. It appears that plants from Texas northward are deciduous and from Mexico southward are evergreen. Observations suggesting the former are (a) the lack of winter or early spring collections from Texas, New Mexico, and Colorado, (b) a collection (*Correll* 29751) in mid-June at a high elevation in western Texas (“base of ledge below Emory Peak”) with flowers all in bud and leaves immature both in texture and size, and (c) the presence of only very young immature leaves on early spring collections of *R. lanceolata*. Evidences of the evergreen condition are (a) a spring collection (*Webster* 146), a March collection (*Rzedowski* 22021) and a January collection from the Federal District (*Pringle* 8055) all with large leaves along a primary axis (presumably from the previous year’s growth) and secondary axes, shorter and with smaller leaves arising from its axils (presumably from the current year’s growth), (b) December and January collections from Guatemala with intact leaves. I found only one exception to this pattern, viz. a February collection from the state

of Mexico (Rzedowski 28825) having only small (immature?) leaves along with flowers that are almost all in bud stage. Wolf (Rancho Santa Ana Bot. Gard Monogr., Bot. Ser. 1: 55. 1938) attributed the deciduous character to *R. smithii* (sensu latiore, including *R. fasciculata*, which I now place under *R. serrata*); he claimed that everything he referred to *R. serrata* was evergreen. However, because we are dealing with plants some of which are found in the temperate zone where strong seasonal changes may affect this character and others are found in tropical mountains where the major seasonal change is from wet to dry, I am unwilling to base taxonomic distinctions on the character expression of deciduous versus evergreen.

Based on averages and appearances, *R. serrata* has longer branchlets at the southern end of its range and shorter branchlets at the northern end; but taken individually, the collections do not always fall into neat categories. For instance, most Coahuila and Texas collections have branchlets not exceeding 5 cm in length, but in five cases out of 18, there are branchlets exceeding 7 cm in length and even up to 11 cm in one case. At the southern end of the range, in San Luis Potosí, branchlets of 5 cm are quite common and roughly half the collections have branchlets of 8 and 9 cm and even up to 12 cm in length; but in the Federal District and state of Mexico, although 5 cm is a rather common length, only one collection has branchlets exceeding 6 cm in length (*Espinosa 710* has branchlets ca. 15 and 30 cm in length and therefore in this respect resembles *R. lanceolata* more than it does *R. serrata*). Therefore, although a tendency can be seen in branchlet length, it is not correlated sufficiently with other characters or localized enough geographically to permit its use in the infraspecific taxonomy.

Because of the superficial appearance of greater crowding of leaves in the two collections (*Hinckley s.n.*) from Mt. Livermore in the Davis Mountains of western Texas and in a group of Coahuila collections, as compared with otherwise similar collections from the Big Bend National Park, Texas, internode length was measured, but the findings were inconclusive. Throughout the range from Chiapas to New Mexico, the most numerous measurements were 1–4 mm, the next most numerous were 5–9 mm and the least numerous were 10–20 mm. The longest internode lengths, as expected, are found in general on the longest branchlets.

Leaf sizes of collections from Mexico, Texas, and New Mexico reveal that *Muller 3188* and *2872* (described by Fosberg as *R. smithii* subsp. *fasciculata* var. *mulleri*), two Rzedowski collections from Hidalgo, and *Espinosa 710* from the Federal District are the only ones with any leaves exceeding 5 cm in length. In this respect they are like *R. smithii* of Colorado and *R. lanceolata* but not like the smaller-leaved plants of Texas and southern New Mexico that Wolf calls *R. smithii* subsp. *fasciculata*. But leaf-size data alone and as a whole do not support segregation of these collections from *R. serrata*. The two Rzedowski collections from Hidalgo have leaves as much as five times as long as wide but the others (notably *Muller 3188* and *2872*) have leaves about 2.5 times as long as wide, a common proportion for

medium-sized leaves throughout the range. Also common is that leaves which measure less than 1 cm are usually 1–1.5 times as long as broad (rarely up to 2.8 times) and are usually proximal on longer branchlets and exclusive on shorter ones. In general, therefore, for *R. serrata* as a whole, there is a gradual decrease in ratios of length to width from upper to lower extremes in length of leaf.

A specimen from New Mexico (*Goodding 6574*) and one from Arizona (*Schroeder s.n.*), which belong to *R. serrata* on the basis of geographic locality, leaf size, and dark-tipped petals, lack the yellowish or brownish coloration of the leaf undersurface. In this respect, they are more like *R. smithii* and *R. lanceolata*.

In the original description of *R. serrata*, the leaves are said to be glabrous. Actually, hairs in variable densities and lengths can sometimes be found, and some degree of geographic correlation can be seen. The undersurface beneath is glabrous in Chiapas, state of Mexico, Hidalgo, Tamaulipas, most Nuevo León, and some Coahuila specimens. Pubescence is sparse to moderate in a few collections from Nuevo León and in most from Coahuila, Chihuahua, Texas, and New Mexico. Long and fairly abundant hairs are common on both surfaces in Texas collections. Such hairs are otherwise found only on the undersurfaces of a few collections from northern Mexico. On the uppersurface, short hairs are common in New Mexico, Nuevo León, and Coahuila collections and in the solitary collection from Chiapas, while hairs are absent commonly in Tamaulipas, San Luis Potosí, the Federal District, and Morelos.

There is some evidence of a geographic gradient in pubescence of nervation of the leaf upper surface. Most collections from the state of Mexico have glabrous nerves. Both glabrous and hairy nerves can be found in San Luis Potosí and Nuevo León, and only hairy ones in Coahuila, Texas, and New Mexico. Tamaulipas and Chihuahua collections apparently fall into the latter category but they are too few for certainty.

Apexes of marginal teeth are exclusively colorless in all collections from the Federal District, state of Mexico (except from *Espinosa 710*), Hidalgo, and San Luis Potosí (except *Pennell 17810*) and in one collection from Tamaulipas, one from Nuevo León, and one from Coahuila. They are amber colored in most New Mexico collections, in that respect resembling *R. smithii*. Dark-colored apexes are seen in all other collections, including the one from Chiapas.

In general, stipule length averages shorter in the northern part of the range and longer from Nuevo León southward, but great variability and overlap occurs, and the character is considered insignificant taxonomically.

Pedicel length of 1–3 mm at anthesis is essentially uniform for all four species with only two exceptions, *Sullivan 590* from Tamaulipas and *Rzedowski 7741* from San Luis Potosí, which have pedicels measuring 4–6 mm. There is no constant distinction between staminate and pistillate flowers in this character.

Because I am defining *R. smithii* and *R. serrata* differently from Wolf,

something must be said about the floral characters that he tried to use to distinguish these two species. According to Wolf, the petals of *R. smithii* are uniformly colored whereas in *R. serrata* they have dark tips. I find exclusively unicolored petals only in *R. lanceolata* and in *R. serrata* var. *guatemalensis*. Otherwise the findings are as follows. *Gooddings* 6574 from New Mexico has dark-tipped petals. *Schroeder s.n.* from Arizona has some dark-tipped and some unicolored petals on the same branch. Among the Texas collections, *Palmer* 34337 (pistillate) and *Correll* 29751 (staminate) have unicolored petals, *Moore & Steyermark* 3161 (staminate; cited by Wolf) has dark tips gradually fading into paler claws, and *Palmer* 30919 (staminate) has the blade somewhat darker than the claw. Among the Mexican collections, some have both unicolored and dark-tipped petals on the same plant with some petals mottled, including *Johnston et al.* 11240 (staminate), *Sullivan* 590 (staminate), *Rzedowski* 7741 (staminate), *Pringle* 8055 (staminate and pistillate; cited by Wolf), *Rzedowski* 2266 (staminate), *Paray* 1907 (staminate), and *Ehrenberg* 979.6 (staminate, cited by Wolf). Other Mexican collections (e.g., *Johnston et al.* 10754) have petals unicolored or with the tip only slightly darker than the claw; and still others have all unicolored petals, including *Graber* 135 (pistillate), *Muller* 455 (staminate), *Purpus* 5330 (pistillate, difficult to interpret; cited by Wolf), and *Rzedowski* 22190 (staminate and pistillate branches). There is slight evidence for a sex correlation from the foregoing data. Female flowers may always have unicolored petals, but male flowers may have either unicolored or dark-tipped petals. The small size of the sample precludes a definitive decision at this time.

Another of Wolf's statements bears rather full discussion. He attributed only unisexual flowers to *R. smithii* (including the New Mexico and Texas populations), and "apparently perfect" ones to *R. serrata*. My own observations suggest that the flowers of all these plants are unisexual. It is possible that they may be protandrous, but the following observations (based on all the flowering specimens of *R. smithii* and *R. serrata* seen) suggest otherwise to me. The apparently staminate flower (judging from the pollen present on the anthers and the small size of the pistil) has the following character-expressions: (a) anther only partially enclosed by the petal, (b) anther 0.5–0.75 mm long, (c) filament 0.5–1 mm long, (d) floral cup 1–2 mm deep, (e) sepals as much as 2 mm long and 1.5 mm broad at base, (f) petals more often dark-tipped than in pistillate flowers, (g) petals 0.6–1.1 mm long and wide, and (h) petal claw broad and indistinct. On the other hand, the apparently pistillate flowers (judging from the well developed pistil and very small anthers) show the following: (a) anther completely enclosed by petal, (b) anther only 0.25 mm long, (c) filament about 0.2 mm long, (d) floral cup 0.6–0.75 mm deep, (e) sepals not exceeding 1.5 mm long and 1.2 mm broad at base, (f) petals more often than not uniform in color, (g) petals only 0.5–0.6 mm long and wide, and (h) claw narrow and distinct. The sample may not have been large enough to serve as a basis for firm conclusions, but the evidence is certainly suggestive.